Review papers

A paleobiogeographical scenario for the Taxaceae based on a revised fossil wood record and embolism resistance

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ABSTRACT

Fossil Taxaceae are documented for the Cenozoic throughout most of the northern hemisphere, but the pre-Cenozoic history of this group is still poorly known. The fossil wood record is difficult but can shed light on this history. We critically evaluated the fossil woods assigned to Taxaceae and then compared the fossil record of taxaceous woods to the fossil record of taxaceous leaves and reproductive structures. We then considered the fossil record in the context of family's molecular phylogeny. More than half of the fossil woods attributed to Taxaceae lack diagnostic characters of the family (longitudinal tracheids with helical thickenings and abietoid pitting on radial walls). Fossil wood that can be attributed to the fossil genus Taxaceoxylon, as well as some specimens placed in the genus Protelicoxylon, which differ only in having mixed type of intertracheary radial pitting, probably belong to Taxaceae. The fossil wood record, as reappraised, is not informative about the history of individual genera within the family, but fits that of leafy remains. Taxaceae wood shows remarkable resistance to embolism and subsequent increased risks of conduit implosion that might be prevented by the presence of tertiary helical thickenings. Our findings suggest a paleobiogeographical scenario for the Taxaceae, that involved a Western Europe Early Jurassic cradle and expansion to their Holarctic modern distribution.

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1. Introduction

The Taxaceae (yew family) is a distinctive family of conifers. Although the family is small, with only 6 genera and 32 species (Farjon, 2010), it is ecologically important, extending widely across the northern hemisphere at mid latitudes (Farjon and Filer, 2013). The family is also of evolutionary and biogeographic interest due to its great age, intriguing distribution, peculiar dispersal strategy (endo-ornithochory) and wide habitat diversity. The family's stem age is likely to be Late Triassic to Early Jurassic and the crown age Mid Jurassic to earliest Cretaceous (Leslie et al., 2012, 2018; Lu et al., 2014; Renner, 2009). The family occurs in diverse habitats from tropical rainforest to high latitude forest. Although a mainly northern hemisphere group, it includes the geographically disjunct genus, *Austrotaxus*, from New Caledonia in the South Pacific (Farjon and Filer, 2013).

Although Florin (1948, 1963) proposed a separate order, Taxales, for Taxaceae, molecular phylogenies clearly place the family within the Coniferales (Rai et al., 2008; Leslie et al., 2012; Ryberg et al., 2012; Yang et al., 2012; Lu et al., 2014). These phylogenies also indicate that *Cephalotaxus* and *Amentotaxus* (once placed in a different family, Cephalotaxaceae) can be considered as part of Taxaceae (Lu et al., 2014; Ghimire et al., 2015). This enlarged Taxaceae is well established as being sister to Cupressaceae *sensu lato* (Rai et al., 2008; Leslie et al., 2012; Ryberg et al., 2012; Yang et al., 2012; Lu et al., 2014).

The fossil record of Taxaceae is sometimes considered poor and difficult to interpret (Taylor et al., 2006; Xu et al., 2015). However, the family's fossil wood record has been little considered. Taxaceae show homogenous and distinctive wood anatomy across the family, except in *Austrotaxus* which has wood that is similar to that of Podocarpaceae (Ghimire et al., 2015). The key anatomical feature of modern Taxaceae wood is that the longitudinal tracheids usually have one to three thin and delicate helices running on the longitudinal walls (Göppert, 1841; IAWA, 2004). These are tertiary thickenings, usually making a variable but typically 45°–60° rarely up to 80° angle with the vertical (axial) direction. As they run along the tracheid, helical thickenings can be followed under light microscopy by adjusting the focus, drawing a low-angle zig-zag pattern. The helix tilt is normally much lower than that of the secondary wall microfibrils of "normal" tracheids (10°–25°) (Fig. 1). As early as 1841, Göppert, on the sole basis of observing helical thickenings, assigned a fossil wood to "*Taxoxylon*" (fossil naming was largely based on supposed affinities at that time).

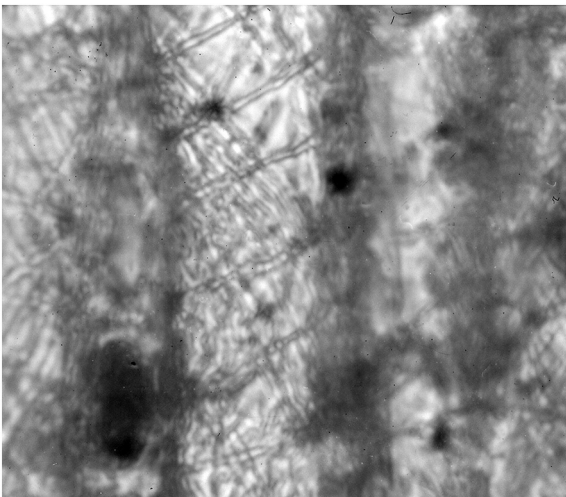Helical thickenings occur in some other conifers, e.g. *Pseudotsuga* (Pinaceae). However, the tracheid wall thickenings in Pinaceae differ from those of Taxaceae in being thinner and more oblique. In addition, Taxaceae are the only extant conifers with the combination of helical thickenings, abietinean intertracheary pitting and smooth ray parenchyma cell walls (Phillips, 1948; for wood anatomy bases see IAWA committee, 2004; Bamford et al., 2016).

The Taxaceae fossil wood record deserves reconsideration. Yew-like fossil woods were reviewed by Kraus (1887), Kräusel (1920), Kräusel and Jain (1964) and more recently Süss and Velitzelos (1994). However, these reviews were incomplete, even the recent one, or are made problematic by some erroneous nomenclatural treatments. In particular, many wood fossils have been assigned to Taxaceae based on inadequate evidence. Moreover, several woods with possible affinities to the Taxaceae (e.g. Afonin and Philippe, 2014) have been recorded subsequent to those reviews.

We therefore review the fossil record for woods supposed to have affinities with Taxaceae. We then compare the fossil wood record with that of leaf and reproductive structures. As the wood of Taxaceae shows high resistance to embolism (Bouche et al., 2014) we discuss the link between this important physiological trait and the family's wood anatomy. These sources of evidence are then combined to propose a paleobiogeographical scenario for the Taxaceae.

2. Materials and methods

2.1. Which genera to consider – a nomenclatural preamble

Fossil conifer wood, i.e., isolated pieces of homoxylous secondary xylem, or tracheidoxyls, are classified into a parataxonomy (Philippe and Bamford, 2008). Thus, only in the exceedingly rare cases of an anatomical connection with leaf or reproductive organs can a fossil tracheidoxyl be assigned with high levels of confidence to a family, except possibly for woods younger than the Paleocene. The wood of extant Taxaceae (except *Austrotaxus*) has three key characteristics: (1) longitudinal tracheids with helical tertiary wall thickenings, (2) mostly abietinean pitting on the radial walls of longitudinal tracheids and (3) smooth ray parenchyma cell walls. After the mid-1960s, most fossil woods with these characteristics were assigned to *Taxaceoxylon* R. Kräusel and Jain, 1964, which is based on material from the Pleistocene of Japan (Kräusel and Jain, 1964). However, several other genera have been used for woods with helical thickenings and abietinean, or mixed or araucarian, intertracheary pitting on the radial wall of their tracheids (TRP thereafter, for "tracheid radial pitting") and have been more or less explicitly claimed to be related to Taxaceae (Bamford et al., 2016). We reviewed all these genera.

The IAWA Softwood List (IAWA Committee, 2004) is our reference for all xylological terms here. The term "helical" is preferred here to the term "spiral", often also used, as a spiral is normally a planar structure.

2.1.1. Fossil wood genera with abietinean radial pitting

At least seven genera of fossil woods (Table 1) are thought to have affinities with the modern Taxaceae because of the occurrence of helical tertiary thickenings and of a mostly abietinean TRP. Although the names *Taxoxylon* Unger, 1842, and its junior homonym *Taxoxylon* Houlbert, 1910, have been widely used to describe yew-like fossil woods, it is unwise to use these names for yew-like fossil woods. Unger (1842) proposed *Taxoxylon* to name a Tertiary fossil wood from Slovakia, previously described by Göppert (1841) as *Taxites scalariformis*. However, the protologue diagnosis of *Taxoxylon* is somewhat ambiguous, the type specimens are poorly preserved, and most seriously, the helical thickenings are artifacts representing crystal chemical zoning patterns (Kraus, 1887, pl. III, fig. 3). In addition, many poorly preserved specimens of dubious affinities have been assigned to *Taxoxylon* (see e.g. Stopes, 1915: 204).

Also *Taxoxylon goeppertii* Unger, the original type species of *Taxoxylon*, is an illegitimate substitute name for *Taxites scalariformis* H.

Fig. 1. *Protelicoxylon lepennecii* Philippe, Early Jurassic of France; here can be seen both a low pitch right-handed helix and steep-pitched microfibrillar pattern due to secondary wall alteration.

Table 1

Summary of nomenclatural and taxonomical features of the genera which were described (p.p. erroneously) as having the diagnostic features of modern Taxaceae wood, i.e., abietinean tracheid radial pitting (TRP); thin-walled, smooth ray parenchyma cell walls; and tertiary helical thickenings in the axial tracheids.

Name	Authorship	Type	Reappraisal	Note
Physematopitys	Göppert (1850)	*P. salisburioides* H.R. Goeppert	Type lost?	Possibly an earlier taxonomical synonym of *Ginkgoxylon* Saporta; type unlocated
Pseudotaxoxylon	Prakash et al. (1995)	*P. chinense* Prakash, Du & Tripathi	Not seen	Both the diagnosis and the illustration mention an araucarian TRP and araucarioid cross-fields; if not resulting from alteration bias the helical thickenings are of the broad *Prototaxoxylon*-type; possibly reworked Paleozoic material; possibly a junior taxonomical synonym of *Prototaxoxylon*
Spiropitys	Göppert (1850)	*S. zobeliana* H.R. Goeppert	Type lost?	Genus described as having both horizontal and vertical resin canals, thus possibly an earlier synonym of *Piceoxylon* Gothan
Spiroxylon	Hartig (1848)	*S. ratzeburgii* Hartig	Type material reviewed by Kräusel (1919)	The type material, poorly preserved, has normal resin canals, hence a genus of dubious circumscription
Taxaceoxylon	Kräusel and Jain (1964)	*T. torreyanum* (Shimakura) R. Kräusel & Jain	Type studied in Tohoku University, Japan	Can accommodate yew-like woods
Taxites	Göppert (1850)	*T. scalariformis* H.R. Goeppert	Not seen	An illegitimate synonym of *Taxites* Brongniart (1828), which stands for leafy twigs
Taxoxylon	Unger (1842)	*T. scalariforme* (H.R. Goeppert) Seward	Type material reviewed by Kräusel (1919) and us	Elliptic diagnosis and poorly preserved type, probably with resin canals
Taxoxylon	Houlbert (1910)	*T. falunense* Houlbert	Type material reviewed by Philippe and Bamford (2009)	An illegitimate junior homonym
Torreyoxylon	Greguss (1967)	*T. boureauii* Greguss	Type material reviewed by Philippe et al. (1999)	From the type material a junior taxonomical synonym of *Agathoxylon* Hartig

R. Goeppert. The name *Taxites* had, however, already been previously used by Brongniart (1828) for twigs with no preserved xylem (*T. tounalii*) from the Oligocene of Southern France. We do not consider it wise to use the same generic name for isolated leafy twigs or secondary xylem pieces when the name is a "form-taxon" (Bateman and Hilton, 2009).

Taxoxylon Houlbert is a validly published junior homonym. However, the type species, *T. falunense* Houlbert, lacks helical thickenings and has been transferred to *Taxodioxylon* (Vaudois-Miéja, 1971). Moreover the syntype specimens for *T. falunense* are poorly preserved (Philippe and Bamford, 2009).

Göppert (1850) also created two other genera *Spiropitys* and *Physematopitys* for fossil wood that he considered to be Taxaceae. *Spiropitys* has been little-used and is today completely forgotten. It is not wise to use this name because the type is not located and its protologue does not have a clear diagnosis. *Physematopitys* was originally supposed to be related to *Ginkgo*, which was then supposed to be related to the yews because of its fleshy ovules.

Hartig (1848) published the name *Spiroxylon*. To the best of our knowledge this name has not been subsequently used. Although the genus is validly published, it is not possible to use it for yew-like fossil woods as the type has non-traumatic resin canals and normal resin canals are not a feature of the Taxaceae (Philippe, 1995). Almost a century later Walton (1925), ignoring Hartig's contribution, used *Spiroxylon* for a South-African wood (*S. africanum*) from the Dwyka or Ecca stages (i.e., Late Carboniferous to Early Permian age). With its obvious araucarian TRP and its thick steep pitched helix, *S. africanum* is probably not closely related to Taxaceae.

In 1967 Greguss established *Torreyoxylon*, which he assigned to Taxaceae. But the araucarian anatomy of the type makes *Torreyoxylon* a junior taxonomical synonym of *Agathoxylon* (Philippe et al., 1999). Although etymologically suggestive, the genus *Protospiroxylon* von Lingelsheim, is for woods with anatomy consistent with *Picea* (Pinaceae), i.e., with thickened and pitted ray-cell walls and ray tracheids (Van der Burgh, 1964). In Prakash et al., 1995 published the genus *Pseudotaxoxylon*, whose diagnosis and protologue illustration include araucarian TRP and araucarioid cross-field pits, hence this genus represents a wood with little affinities to modern yew woods. The diagnosis of the more recently described *Sommerxylon* (Pires and Guerra-Sommer, 2004) includes features of the primary structures (pith, primary xylem). Consequently, it cannot be used to name tracheidoxyls. Similarly, *Herbstiloxylon* Gnaedinger *in* Gnaedinger & Herbst is designed

for *Protelicoxylon*-type of secondary xylem associated with primary structures (Gnaedinger and Herbst, 2006). Without explanations Zheng et al. (2008) assigned *Brachyoxylon* Hollick & Jeffrey to the Cephalotaxaceae, but the type of this genus wood lacks tertiary helical thickenings.

2.1.2. Genera with mixed type of radial pitting

Three genera were used for woods described as having helical tertiary thickenings and mixed type of TRP (Table 2): *Platyspiroxylon* Greguss, 1961; *Protelicoxylon* Philippe, 1995; and *Prototaxoxylon* R. Kräusel and E. Dolianiti, 1958. Their anatomy is somewhat similar to that of *Protocallitrixylon* Yamazaki and Tsunada, 1982.

The type species of *Platyspiroxylon* (*P. heteroparenchymatosum* Greguss) is definitely araucarian in its TRP, as is the second species included by Greguss in 1967 (Philippe et al., 1999). The genus is thus a junior taxonomical synonym of *Prototaxoxylon* R. Kräusel & Dolianiti. According to Greguss (1967) himself, who favored a link with *Callitris* (Cupressaceae), *Platyspiroxylon* is not related to the Taxaceae. Later, however, Prasad (1986) compared *Platyspiroxylon* and *Prototaxoxylon* and used the former name for woods with a TRP said to be of the mixed type.

Although some woods with mixed type of TRP have been assigned to *Prototaxoxylon* (e.g. Fakhr and Marguerier, 1977), it seems wiser to keep this genus for tracheidoxyls with completely araucarian TRP as in the *Prototaxoxylon* type, *P. africanum* (Walton) R.Kräusel & E. Dolianiti, and in accordance with the original diagnosis which states "*radial pits never perfectly round or opposite*".

Protocallitrixylon was described twice as a new genus, first by Yamazaki and Tsunada (1982) and then by Vozenin-Serra and Salard-Cheboldaeff (1992). The first description is validated by a *diagnosis generico-specifica* (ICBN, art. 38.5) based on *P. liassicum* Yamazaki & Tsunada. These authors simultaneously described a "sp. A" and a "sp. B", however since the Sydney Code in 1981 a "monotypic genus" is understood as one for which a single binomial is validly published even though the authors may indicate that other (unnamed) species belong to the genus. Yamazaki & Tsunada described this genus as having araucarian to mixed-type TRP. Independently, Vozenin-Serra & Salard-Cheboldaeff described *Protocallitrixylon*, but with abietinean TRP and axial parenchyma. Both types (resp. *P. liassicum* and *P. kanakense*) have helical thickenings, but these are predominantly of the callitroid type, paired and transversal, not running on all tracheid faces. No *Protocallitrixylon* species seem related to the Taxaceae.

Table 2
Summary of nomenclatural and taxonomical features of the genera which have been used for yew-like fossil woods with mixed type tracheid radial pitting (TRP) and helical thickenings.

Name	Authorship	Type	Reappraisal	Note
Platyspiroxylon	Greguss (1961)	*P. heteroparenchymatosum* Greguss	Type material reviewed by Philippe et al. (1999)	A junior taxonomical synonym of *Prototaxoxylon* R.Kräusel & Dolianiti
Protelicoxylon	Philippe (1995)	*P. feriziense* (Fakhr & Marguerier) Philippe	Type not seen	
Prototaxoxylon	Kräusel and Dolianiti (1958)	*P. africanum* (Walton) R. Kräusel & Dolianiti	Type material reviewed by Kräusel and Dolianiti (1958)	Should not be used for woods with mixed type of TRP. Helical thickenings broad and at a 30°–40° angle with the tracheid axis.

2.1.3. Genera with araucarian type of radial pitting

Numerous genera were occasionally said to be related to Taxaceae although they have been proposed for woods described as having araucarian TRP and tertiary thickenings, associated or not with primary structures: *Palaeospiroxylon* Prasad & Chandra, 1980; *Parapalaeospiroxylon* Pant & Singh, 1987; *Parataxopitys* Maniero, 1951; *Platyspiroxylon* Greguss; *Prototaxopitys* Agashe, 1977; *Prototaxoxylon* R. Kräusel & Dolianiti; *Sinopalaeospiroxylon* Zhang, Wang, Zheng, Yang, Li, Fu & Li, 2007; *Sommerxylon* Pires and Guerra-Sommer, 2004; *Spiroxylon* Walton; *Taxopitys* R.Kräusel in R.Kräusel & Range, 1928. These usually have bi-multiseriate radial bordered pits and their helical thickenings are usually thick, making an angle with the longitudinal direction usually not exceeding 40° (steep pitch). These woods are mostly reported from the Paleozoic (late Carboniferous–Permian interval) and are typically Gondwanan (Mehta, 1952; Agashe and Shashi Kumar, 2002; Berthelin et al., 2003).

As both the Taxaceae and their sister-group the Cupressaceae have abietinean to weakly mixed TRP-type, fossil woods with typically araucarian TRP are probably not closely related to Taxaceae. Hence, we do not consider further *Palaeospiroxylon*, *Parapalaeospiroxylon*, *Parataxopitys*, *Platyspiroxylon*, *Prototaxoxylon*, *Sommerxylon*, *Spiroxylon* and *Taxopitys*, except for the few Mesozoic woods which were attributed to these genera. Indeed, as the core of this group belongs to the Paleozoic, Mesozoic woods might have been misidentified.

Here mentioned fossil woods are referred to, as much as possible, under their basionym, without prejudging the merit of published (or to be published) taxonomical arguments in favor of a renaming.

2.2. Causes for misinterpreting presence of helical thickenings

There are multiple types of structures that are known to be easily confused with helical thickening (e.g. Kraus, 1887; Gothan, 1905; Shimakura, 1936). Despite this, numerous authors have been fooled, even recently. Tunneling bacteria, fungal attacks, differential mineral impregnations or shrinking cracks induced by wood diagenesis can all emphasize the microfibrils and create oblique structures that may be confused with helical thickenings (Fig. 2). The microfibrillar patterns involved in these cases usually consist of several closely parallel strikes which usually do not curve towards the tracheid face rim. These strikes are at a variable angle with the longitudinal axis. This is well illustrated by Araujo et al. (Araujo et al., 2011, fig. 6F).

Compression wood longitudinal tracheids have checks in their walls that when observed with optical microscopy can be confused with helical thickenings (Boyd, 1973). The microfibril angle of compression wood tracheids is usually 30°–50° from the longitudinal axis, unlike "normal" tracheids with a predominant 10°–20° angle (Timell, 1986). Also, the tips of these cracks are usually pointed and straight, whereas it is not the case for the true helices. Such diagonal patterns, mentioned as checks or cracks, are well illustrated by Hickey et al. (2011). In some compression wood, borders around pits are usually small, while the pit aperture opens in tracheid lumen at the bottom of an oblique furrow. Such furrows have also been erroneously described as tertiary thickenings, especially when broadened by wood shrinkage during diagenesis (see Greguss, 1967 pl. 35, fig. 19b). They characteristically make a low angle with the tracheid longitudinal axis, usually 30°–40°, are much broader than the true helical thickenings and have an aperture in their middle. In fossil woods with such patterns, the pale (supposedly "thin") band is usually as broad as the dark (supposedly "thickened") band under optical microscopy, while a pit set on the opposite tracheid wall can sometimes be seen behind the banded pattern (Fig. 3). This appearance is especially common in silicified araucaria-like woods. In a few cases, (e.g. Yamazaki et al., 1979, pl. IV) it is difficult to judge if some structures are yew-like helical thickenings or relatively thick bands sandwiched between two oblique furrows. The angle could then be diagnostic. Intensity of taphonomic processes seems to enhance diverse oblique structures (Evans, 1928).

Zoned patterns in some petrified fossil woods, caused by discontinuous crystal growth have several times been confused with helical thickenings (see e.g. Kraus, 1887; Houlbert, 1910 and Philippe and Bamford, 2009; Fig. 4). These patterns are, however, made of closely parallel but irregularly spaced lines.

Crystal cleavage plans can also be tricky, however they normally run across several tracheids.

Fungal hyphae can mimic grooves within a tracheid because hyphae often follow the S2 cell wall layer (see Greguss, 1967, pl. 32), however their disposition is rarely regular enough to convincingly suggest tertiary thickenings.

In extant *Taxus* and *Pseudotsuga* species helical cavities can occur within the tracheid wall, which curiously seem to be mutually exclusive with helical thickenings (Timell, 1978).

To sum up, it is easy to mistakenly interpret various oblique patterns in the tracheids as helical thickenings, as Kraus (1887) warned earlier. Later, in 1936, Shimakura wrote "*As pointed out by Kraus, Lingelsheim, Seward, Stopes, Gothan and Kräusel, there are no true spiral thickenings in most species of* Taxoxylon *or* Taxites". Although numerous publications have warned that such helices can be mistakenly diagnosed, Shimakura's statement is still today quite true. Scanning electron microscopy is a good means to determine whether or not helical wall thickenings are truly present (Philippe et al., 1999; Wan et al., 2016).

2.3. Fossil woods with helical tertiary thickenings – a database

We surveyed the paleoxylological literature for woods said to be related to Taxaceae. Based on previous information we focused on the genera whose anatomy conforms to modern Taxaceae, i.e. *Platyspiroxylon* Greguss, *Protelicoxylon* Philippe, *Prototaxoxylon* R. Kräusel & E.Dolianiti, *Sommerxylon* Pires & -(Guerra-Sommer), *Taxoxylon* Houlbert, *Taxoxylon* Unger, *Taxaceoxylon* R.Kräusel & Jain and *Torreyoxylon* Greguss. Paleozoic woods with strongly araucarian radial TRP and helical thickenings were not considered (e.g. *Taxopitys*, *Parataxopitys*). We also excluded *Oguraxylon* Nishida which has traumatic resin canals and axial parenchyma, features that are not reported for modern Taxaceae. We focused on the Mesozoic as this is a major phase in the radiation of conifers, with the establishment of basal genera (Leslie et al., 2012, 2018).

We located 61 records for 57 taxa. For each record we questioned the possibility that the described material was reworked, especially for fossils in alluvial sediments. As far as possible we examined the type material, to limit interpretation bias, and all protologues were accessed. Our database is complete to the best of our knowledge. Should some
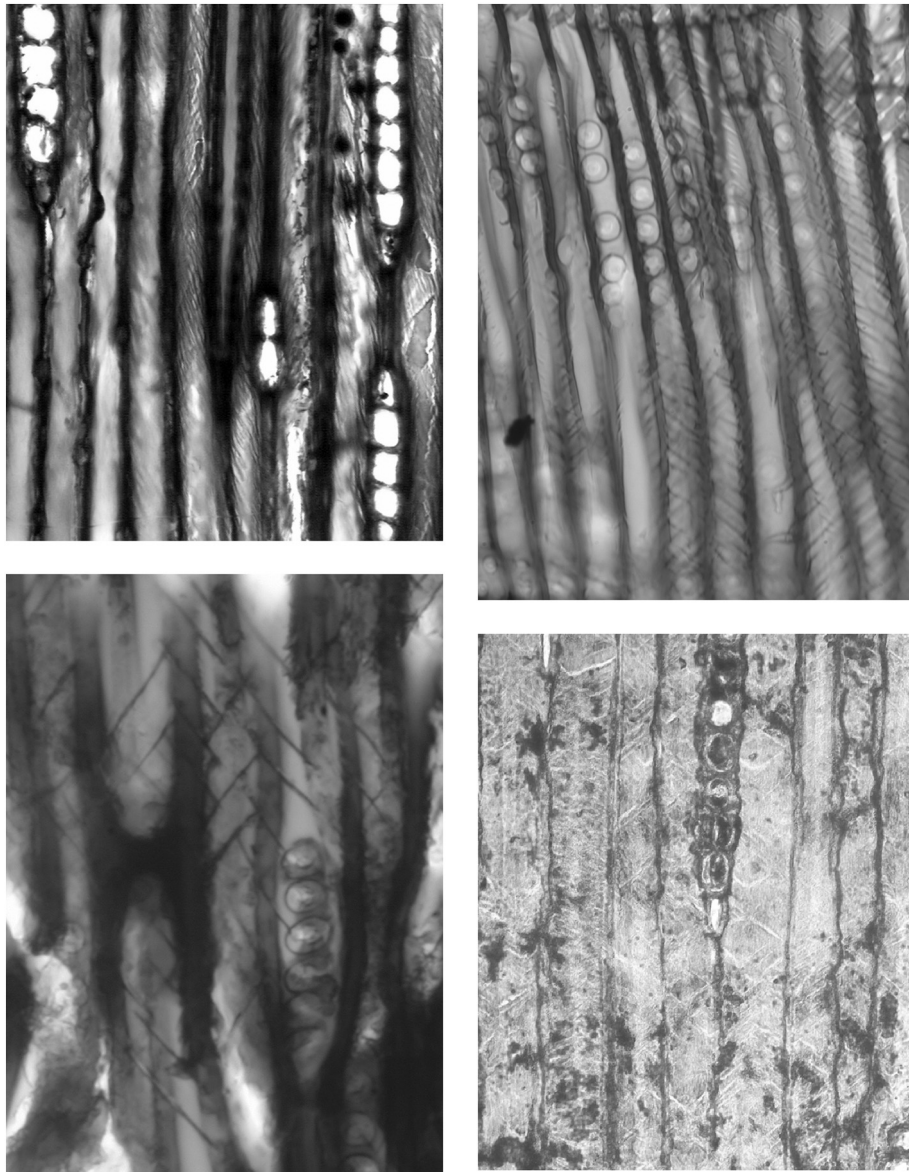
Fig. 2. Confusing spiral-like patterns. (A) *Podocarpoxylon woburnense* Stopes, sample 58481 in British Museum of Natural History; steep angled microfibrillar pattern resulting from tracheid secondary wall differential attack. (B) V13139 in British Museum of Natural History; low angled similar microfibrillar pattern, within a compression wood. (C) V16556a in British Museum of Natural History; cleavage fractures running through tracheid walls in a mineralized wood. (D) *Pityoxylon woodwardii*; oblique patterns interpreted as resulting of tunneling bacteria activity.

papers have been forgotten, we would be very grateful to get notice. We are confident that no significant data were overlooked.

3. Results

From our reappraisal 12 of the 61 records were assigned to the *Prototaxoxylon* group (araucarian TRP, thick helices with a steep pitch; Table 3), 6 to *Protocallitrixylon* (mixed type of TRP, thin low pitch helices plus callitroid thickenings, Table 4), 8 to *Protelicoxylon* (mixed type of TRP, thin low pitch helices; Table 5) and 11 to *Taxaceoxylon* (abietinean TRP, thin low-pitch helices, no callitroid thickenings; Table 6). Only these three last genera will be considered further. An extra group is recognized for seven woods from India (Table 7). As the analysis did not unequivocally support assignment to one of the five groups cited here, the above 43 records were discarded (Appendix).

Because of their araucarian radial tracheid pitting several Mesozoic woods belong to *Prototaxoxylon*. It is striking that they are limited to

the Gondwana, where they mostly occur at high paleolatitudes (Table 3 and Appendix).

Except for the New-Caledonian data (Vozenin-Serra and Salard-Cheboldaeff, 1992), *Protocallitrixylon* woods form a spatiotemporally coherent unit (Table 4). They are distributed exclusively in the Far-East Asia, from the Early Jurassic to the Early Cretaceous. First encountered at low to mid paleolatitudes, their range subsequently shifted northward, within an area characterized by a cold-temperate flora (Oh et al., 2011). The occurrence of the genus in the Teremba terrane of New-Caledonia is questionable, as most paleogeographic reconstructions have this area at the southern rim of a wide open oriental Tethys (Cluzel et al., 2012) during the Jurassic.

Protelicoxylon woods, as here revised, form another spatiotemporally coherent unit (Table 5). They are distributed exclusively in Eurasia, from the Early Jurassic to the Mid-Jurassic–Early Cretaceous. First encountered in Western Europe, their range apparently shifted eastward. The exact age of the Cambodian data is unfortunately not well constrained (Philippe et al., 2004). *Protelicoxylon* is not reported to

Fig. 3. Formation of a large spiral-like ribbon from araucarian radial pitting. (A & B) *Xenoxylon wattarianum* Nishida holotype, Chuo University; two alteration stages in the same slide. C - *Xenoxylon phyllocladoides* sample no 686901. Symmetrical transitions, in two adjacent tracheids, from araucarian radial pitting to a broad spiral pattern.

have co-existed with *Protocallitrixylon*. In Iran, it co-occurs with *Xenoxylon* Gothan (Nadjafi, 1982), a paleoecologically significant genus that indicates relatively wet settings (Philippe et al., 2017).

First appearance date for the genus *Taxaceoxylon* is the Early Cretaceous. At that time it was exclusively distributed in North-Eastern Eurasia. By the Late Cretaceous it occurred in Northern America, and in the Tertiary it was distributed throughout the Palaearctic (Table 6).

A set of woods from India is questionable. Most of them have convincing illustration for helical thickenings but poorly preserved TRP (Table 7). In 1952 Bose described *Brachyphyllum spiroxylon* from the Rajmahal Hills, Jharkhand, India. The type material is a leafy twig with *Brachyphyllum*-like foliage, 4 mm in diameter, however it is described as having a wood of the *Taxaceoxylon*-type. Unfortunately, the cross-field pitting is not preserved, and TRP is observed only in juvenile wood. Also, helical thickenings were not observed in the tangential section. These Indian woods can further be subdivided into two subgroups, one from the earliest Jurassic of Central India (Eastern Maharashtra/Northern Andhra Pradesh), and another from the Early Cretaceous of Western India (Jharkhand). These two groups correspond to the two main Mesozoic wood provenances in India studied to date.

4. Discussion

The wood fossil record includes many Mesozoic and Cenozoic specimens with some Taxaceae anatomical features. Only wood having helical thickenings and abietinean pitting (i.e. wood that is, or should be, assigned to *Taxaceoxylon*) is convincingly Taxaceae, although some other wood types (e.g. *Protocallitrixylon* and *Protelicoxylon*) may represent ancestral forms of the Taxaceae lineage. The record shows that five taxonomically and spatiotemporally well-circumscribed groups can be recognized among the Mesozoic or younger fossil tracheidoxyls with helical thickenings.

The first group has steep and wide thickenings and araucarian TRP. It occurs in Gondwana, mostly at high paleolatitudes, and mostly in the Jurassic. It is anatomically close to the Paleozoic *Prototaxoxylon* and will be referred to hereafter as "Mesozoic *Prototaxoxylon*". It is possible that *Sommerxylon* is related to this group.

The two next groups have a mixed type of TRP. One (*Protocallitrixylon*) has both callitroid and helical thickenings; it is limited to the Mesozoic of far-east Asia and New-Caledonia. The fourth group (*Protelicoxylon*) is documented from Eurasia, only from the Mesozoic, and mostly from the Jurassic. Wood fossils similar to the wood of extant Taxaceae (*Taxaceoxylon*) are encountered throughout the Palearctic, from the Early Cretaceous to the Pleistocene. A fifth group, only
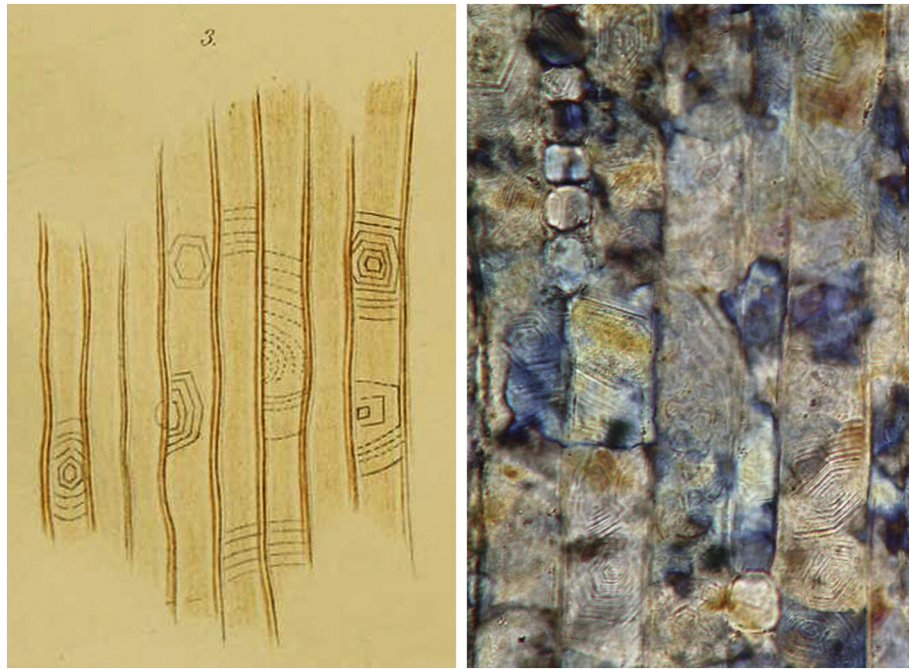
Fig. 4. Left, reproduction of pl. III fig. 3 in Kraus (1887), warning about misinterpretation of crystal patterns; right, *Taxoxylon falunense* Houlbert, sample no 25 in the Musée du Grand-Pressigny, Indre-et-Loire, France.

encountered in the Mesozoic of India, has Taxaceae-like helical thickenings, and possibly mixed type of TRP (most of them have no preserved pitting).

This five group scheme is compared to the leaf and reproductive organ record for Taxaceae. This leads to the idea that only *Protelicoxylon* and *Taxoxylon* probably belong to Taxaceae. Furthermore, we propose that the helical thickenings of Taxaceae tracheids may contribute to the family's very high resistance to hydraulic failure because – as observed in *Acer* species by Lens et al. (2011) – the more pronounced the thickenings on inner vessel walls, the more embolism resistance the species. However, the functional role of vessel wall thickening is

still poorly understood and further research needs to be carried out to unravel its role in drought resistance. We here speculate that wall thickening does not play a direct role in preventing embolism formation but instead is involved in preventing xylem implosion. We then integrate the fossil record, estimated resistance to water stress and Meso-Cenozoic paleoclimatology to create a biogeographic hypothesis.

4.1. Comparison of wood with the leaf and reproductive organ fossil record

Taylor et al. (2006) concluded that it is difficult to trace the origin of Taxaceae from the fossil record of leaf, leafy twigs or reproductive
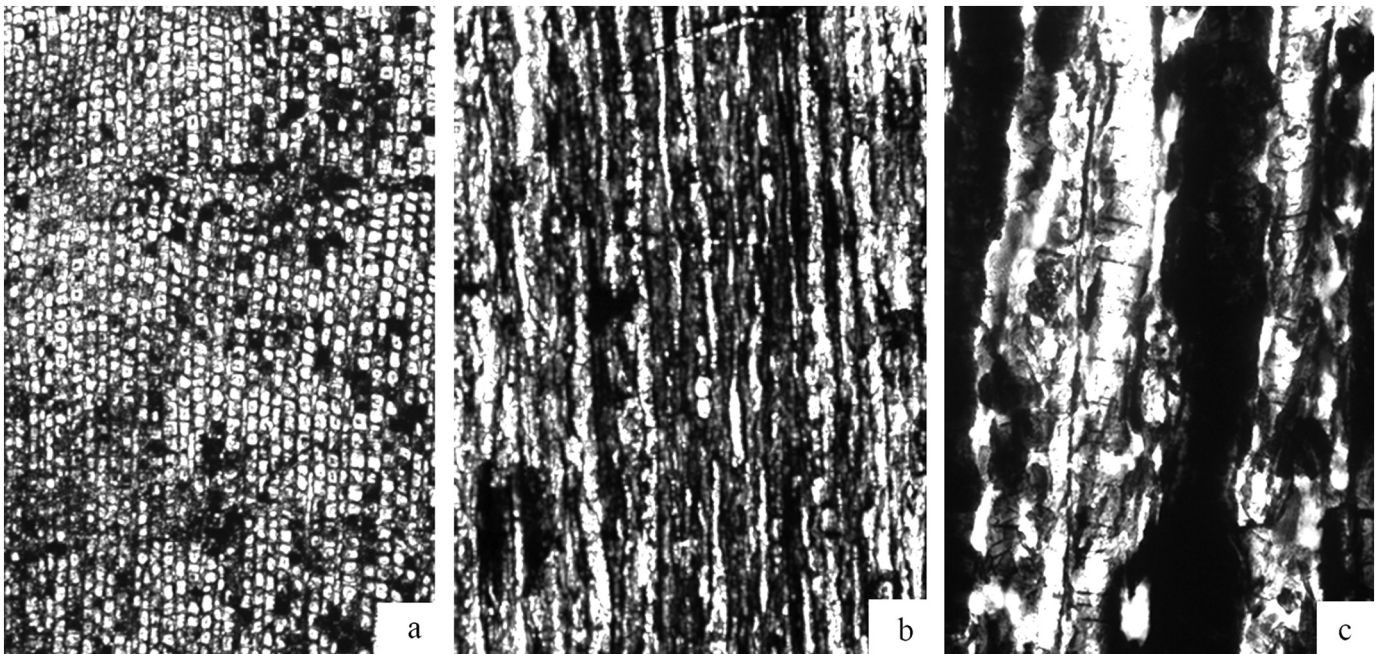
Fig. 5. Wood assigned to genus *Protocallitrixylon*, unpublished wood collected by Kazuo Terada, sample no FPDM-P-1130 in Fukui Prefectural Dinosaur Museum, Japan; Early Cretaceous, Kitadani Fm, Tetori Group, Japan.

Table 3
Fossil woods described as having helical tertiary thickenings and araucarian type of pitting on tracheid radial walls and which are consistent with the genus *Prototaxoxylon* Kräusel & Jain.

Taxon name, authority	Reference
Protelicoxylon feriziense (Fahkr & Marguerier) Philippe	Gnaedinger and Herbst (2006)
Prototaxoxylon acevedoae Gnaedinger & Herbst	Gnaedinger and Herbst (2006)
Prototaxoxylon intertrappeum (Prakash & Srivastava) Prakash & Srivastava	Lutz et al. (1999)
Prototaxoxylon intertrappeum (Prakash & Srivastava) Prakash & Srivastava	Gnaedinger and Herbst (2006)
Prototaxoxylon uniseriale Prasad	Gnaedinger and Herbst (2006)
Sommerxylon spiralosus Pires & Guerra-Sommer	Pires and Guerra-Sommer (2004)
Taxaceoxylon cupressoides Sharma	Sharma (1971)
Taxaceoxylon sahnii Rajanikanth & Sukh-Dev	Rajanikanth and Sukh-Dev (1989)
Taxaceoxylon sp.	Mahabale (1967)
Taxaceoxylon sp.	Caminos et al. (1995)
Taxoxylon sp.	Lakhanpal et al. (1976)
Wood of type D	Yamazaki et al. (1979)

organs only. The characteristic fleshy arils have little potential for fossilization, and none have been described from the Mesozoic or Paleozoic (non-fleshy, or perhaps immature, arils have been described from putative Middle Jurassic Taxaceae like *Marskea* and *Proteridion*). Moreover, podocarp reproductive organs (epimatia) share a similar gross morphology with that of the Taxaceae, and it is difficult to tell apart an epimatium and an aril from fossil remains only. To compound the problem, the recent suggestion that Gnetales could be sister to the Pinaceae family (Bowe et al., 2000) suggests that a fleshy structure, whatever its ontogeny, can relatively easily be invented by the gymnosperms, and could have been present in some of the numerous little-known Mesozoic gymnosperm families (e.g. Ferugliocladaceae or Buriadaceae). Thus a fossil fleshy aril would probably not be unequivocal evidence of Taxaceae.

Although foliage of Taxaceae is more likely to be preserved than the arils, the gross morphology of shoots and leaves of this family is little differentiated from that of several other conifer clades. As a result, leaf and leafy twig fossils are largely uninformative when cuticle is missing. The cuticle is distinctive for modern genera (Elpe et al., 2017), although Taxaceae cuticle can resemble that of some completely unrelated taxa, e.g. within the Monocots (Conran, 1997). Similarly, Jordan et al. (2011) observed Taxaceae-like cuticle in fossil *Phyllocladus* (Podocarpaceae).

Several fossil genera based on foliar specimens and with relatively well-established affinities to the Taxaceae, e.g. *Marskea*, *Palaeotaxus*, *Poteridion*, *Thomasiocladus* (Taylor et al., 2006; Xu et al., 2015) have been described from the Jurassic. These genera are only reported from

Table 4
Fossil woods with helical tertiary thickenings, mixed type pitting on tracheid radial walls and callitroid thickenings, here accepted as belonging to the genus *Protocallitrixylon* Yamazaki & Tsunada. The nov. comb. *Protocallitrixylon pulchrum* is based on the basionym *Taxoxylon pulchrum*, He Dechang, *The coal forming plants of Late Mesozoic in Dan Hinggan Mountains*, p. 13, pl. 8, figs. 3–3a, pl. 9, figs. 1–1f; 1995.

Taxon name, authority	Reference
Protocallitrixylon kanakense Vozenin-Serra & Salard-Cheboldaeff	Vozenin-Serra and Salard-Cheboldaeff (1992)
Protocallitrixylon liassicum Yamazaki & Tsunada	Yamazaki and Tsunada (1982)
Protocallitrixylon pulchrum (He Dechang) nov. comb.	He Dechang (1995)
Protocallitrixylon sp. A	Yamazaki and Tsunada (1982)
Protocallitrixylon sp. B	Yamazaki and Tsunada (1982)
Protocallitrixylon sp.	this work; Fig. 5

Eurasian mid-paleolatitudes. In this respect, they fit well with known spatiotemporal distribution of *Protelicoxylon*, albeit they have not yet been recorded as far east as the latter along Tethys northern rim. The record of above-mentioned foliar fossil genera starts with *Palaeotaxus* from the Earliest Jurassic (Florin, 1958), which also fits with first *Protelicoxylon*, documented from the Hettangian.

A striking feature is that by the Early Cretaceous the record of Taxaceae fossil foliage record is centered on much higher paleolatitudes. Although there are putative records from Belgium (Alvin, 1960), UK (Watson et al., 2001) and North Carolina (Berry, 1910), the strongholds are at higher paleolatitudes than any presumed Jurassic records of the family: Greenland (Heer, 1883), Siberia (Krassilov, 1976; Samylina, 1988; Golovneva, 1994; Bugdaeva et al., 2006), Spitzbergen (Bose and Manum, 1990), north-eastern China (Xu et al., 2015). There is thus a similar northward shift for both leaf and reproductive organ record and wood record during the Jurassic–Cretaceous interval. This shift is concomitant with abietinean TRP becoming dominant in wood.

By the Cenozoic the Taxaceae were widespread over high latitude regions of the Northern Hemisphere, with fossil foliage records in North-America (e.g. Kvaček and Rember, 2007), Europe (e.g. Givulescu, 1973; Ferguson, 1978; Ferguson et al., 1978; Kvaček, 1986; Spjut, 2007; Macovei, 2013) and Asia (Xu et al., 2015). This Cenozoic distribution fits again with that of fossil wood record.

The enigmatic *Austrotaxus* has no fossil record of any kind. As its wood is similar to that of the Podocarpaceae (Bobrov et al., 2004), isolated secondary xylem of this genus would probably be referred to *Podocarpoxylon* Gothan, which is not considered here. Thus, the fossil wood record cannot be used to improve an understanding of the biogeographic history of this taxon.

4.2. Helical thickenings and drought resistance

Extant Taxaceae, especially *Cephalotaxus*, have a relatively high resistance to embolism (Delzon et al., 2010; Bouche et al., 2014; Fig. 6). Thus, extant Taxaceae, with the notable exception of *Austrotaxus spicata*, have a lower P_{50} (i.e. greater resistance) than all Araucariaceae, all basal Cupressaceae and most species of Pinaceae and Podocarpaceae. Only a few genera of the Cupressoid and Callitroid clades of Cupressaceae have lower wood xylem P_{50} than *Cephalotaxus*: the *Callitris* clade being by far the most embolism resistant group of trees in the world (Brodribb et al., 2015; Larter et al., 2015, 2017).

Tracheids of embolism resistant species often experience low water potentials, increasing the risk of conduit implosion (collapse), that could compromise the function of the xylem. Collapse of xylem conduit walls during desiccation was reported in pine needles (Cochard et al., 2004). This concept extends to conifer wood because the pressure needed to cause conduit implosion in lignified tracheids (estimated with the double cell-wall thickness) is related to embolism resistance across conifers (Bouche et al., 2014). Furthermore, collapse of xylem conduit walls in response to desiccation has been observed in some Pinaceae wood with severe reduction of lignification in their secondary walls (Barnett, 1976; Donaldson, 2002) and in pine needles (Cochard et al., 2004). Vulnerability to collapse is therefore highly related to the tracheid anatomy. *Taxus*-like helices could be interpreted as a trade-off between physiologically costly thick lignified walls, water transport and drought resistance. Tracheid helical-thickenings would allow thinner cell walled tracheids to have similar mechanical resistance to collapse (Roth-Nebelsick and Speck, 2000), while having a wider lumen, i.e. being more efficient to transport sap. In fact, xylem wall collapse has been reported in several species between the helicoidal thickening (Johnson, 1977; Turner and Somerville, 1997; Cochard et al., 2004).

It is striking that both extant conifer taxa (Taxaceae and Callitroideae) with abundant tertiary thickenings in their woods have high resistance to embolism (Fig. 6). Furthermore, the only genus of Taxaceae without tertiary helical thickenings, *Austrotaxus*, is the most vulnerable species to embolism in the family. These findings suggest

Table 5
Fossil woods with helical tertiary thickenings and mixed type pitting on tracheid radial walls, here assigned to the genus *Protelicoxylon* Philippe.

Taxon name, authority	Reference	Age	Country
Protelicoxylon asiaticum (Serra) Philippe	Serra (1969)	Early? Cretaceous	Cambodia
Protelicoxylon feriziense (Fakhr & Marguerier) Philippe	Fakhr and Marguerier (1977)	Middle Jurassic	Iran
Protelicoxylon lepennecii Philippe	Philippe (1995)	Toarcian	France
Protelicoxylon parenchymatosum (Greguss) Philippe	Greguss (1967)	Toarcian	Hungary
[*Prototaxoxylon persicum*]	Nadjafi (1982)	Early to Middle Jurassic	Iran
Protelicoxylon sp.	Barbacka and Philippe (1997)	Hettangian	Hungary
Protelicoxylon sp.	Philippe et al. (2006)	Sinemurian	Romania
Protelicoxylon sp.	New data	Toarcian	France (Nancy)

that helical thickenings may play a role in preventing conduit implosion in high resistant species to embolism.

The high resistance to embolism is interesting because extant Taxaceae are rather mesophytic trees and shrubs, which may also be the case for most of their Cenozoic ancestors (Ferguson et al., 1978). However, this is in line with other physiological adaptations to drought observed in the Taxaceae (Hoffman et al., 1999; Feucht et al., 2012). Extant Taxaceae trees and shrubs are all shade tolerant. Their resistance to drought, together with their shade tolerance strategy, might have allowed Taxaceae to establish under angiosperm-dominated canopies.

4.3. A paleobiogeographical scenario for the Taxaceae

Phylogeny of the Taxaceae genera and the supposedly monotypic family Cephalotaxaceae has been extraordinarily controversial (Cheng et al., 2000). Molecular phylogenies now converge to give a more consensual image (Fig. 7). Taxaceae are considered monophyletic, splitting from the sister-group, the Cupressaceae, during the Late Triassic or earliest Jurassic. *Cephalotaxus* branched during the Early to Middle Jurassic and the division between the two remaining clades of Taxaceae occurred during the Middle to Late Jurassic, one clade containing *Torreya* and *Amentotaxus*, the other *Austrotaxus*, *Pseudotaxus* and *Taxus* (Cheng et al., 2000; Renner, 2009; Leslie et al., 2018).

If the Mesozoic *Prototaxoxyla* are not considered safe evidence of Taxaceae, the fossil wood record fits well with the image drawn by molecular phylogeny. With the Hettangian (Earliest Jurassic, ca. 200 Ma) as its first appearance date, *Protelicoxylon* fits with a first radiation of the Taxaceae within the Late Triassic/Early Jurassic. Accordingly, from the fossil wood record it can be hypothesized that Taxaceae appeared in Western Europe at the T/J boundary.

Evolutionary ecophysiology suggests that Triassic conifer stem groups had a limited resistance to embolism (Pittermann et al., 2012; Larter et al., 2017). It further suggests that resistance gradually increased for the Taxaceae during the Jurassic and likely had reached modern values by the end of the Cretaceous at 65 Ma (Larter, 2016). This age fits well with our taxonomical inferences, with intermediate and untypical woods classified here as *Protelicoxylon* appearing during the Jurassic, and typical *Taxaceoxylon* appearing during the Early Cretaceous, at higher and drier paleolatitudes. During all the Mesozoic, at least, Taxaceae family seems to have evolved under a strong constraint to become more drought resistant. This evolution was parallel to a transition from a mixed type of TRP to an abietinean TRP. It is probable that this change in the TRP had consequences on conduction. This northward shift of the (*Protelicoxylon* + *Taxaceoxylon*) group during the Jurassic–Early Cretaceous interval fits well with a well-documented global poleward shift of the at least seasonally dry temperate climate zone (Hallam, 1985).

According to the phylogeny of Fig. 7 (based on Leslie et al., 2018) the stem group of the most embolism resistant genus of Taxaceae, *Cephalotaxus*, evolved at the end of the Early Jurassic and the crown group in the late Cenozoic. So the highly resistant wood may have evolved any time in this period. Thus, the Cretaceous record is entirely consistent with late evolution of resistance.

Austrotaxus radiated during the Early Cretaceous and remained highly isolated (Leslie et al., 2018). Thus, it is improbable that *Austrotaxus* is related to the Triassic *Protocallitrixylon* described from New-Caledonia by Vozenin-Serra and Salard-Cheboldaeff (1992). It might be derived from *Protocallitrixylon* which occurred during the Jurassic in South-Eastern Asia, however, the possibility of terrestrial species migration along the Eastern Tethys at that time is controversial (Vozenin-Serra, 1977). *Austrotaxus* is clearly divergent from the rest of the Taxaceae, in both wood anatomy and resistance to embolism, and also in the diffuse type of branching and plagiotropic branch growth (Chomicki et al., 2017). According to the phylogeny of Leslie et al. (2012) or Lu et al. (2014), both the Taxaceae-type wood anatomy and xylem resistance to embolism were either lost secondarily in *Austrotaxus* or evolved convergently in two clades (Fig. 7). It is noteworthy that it is endemic to New-Caledonia, a center of diversity for Araucariaceae (Farjon, 2010), a family with a high vulnerability to embolism (Fig. 6). In no fossil flora is *Taxaceoxylon* found associated with *Agathoxylon*, the wood fossil genus fitting with modern Araucariaceae, as if in the past these two groups always had different ecological requirements. The extant *Austrotaxus* case opens the possibility that some fossil woods assigned to *Podocarpoxylon* (e.g.), and possibly associated with *Agathoxylon*, might be cryptic Taxaceae woods lacking tertiary helical thickenings. The *Austrotaxus* thinner ray-cell walls, as compared to the other family members, might also be in line with a lower resistance to embolism.

Table 6
Fossil woods with helical tertiary thickenings and abietinean type pitting on tracheid radial walls, here considered assignable to the genus *Taxaceoxylon* Kräusel & Jain. The nov. comb. *Taxaceoxylon antiquum* is based on *Torreya antiqua* Boeshore & Gray, *Amer. J. Bot.* 28, p. 525, textfigs. 1–14, 1936 (not validly published in Pires and Guerra-Sommer, 2004).

| Taxon name, authority	Reference	Age	Country
Taxaceoxylon antiquum (Boeshore & Gray) nov. comb.	Boeshore and Gray (1936)	Late Cretaceous	USA (Eastern)
Taxaceoxylon biseriatum Süss & Velitzelos	Süss and Velitzelos (1994)	Tertiary	Greece
Taxaceoxylon jarmolenkoi Shilkina	Shilkina (1989)	Early Cretaceous	Russia (Western)
Taxaceoxylon liaoxiense Duan	Duan (2000)	Early Cretaceous	China (Northern)
Taxaceoxylon saghalienense H. Nishida et Nishida	Nishida and Nishida (1986)	Late Cretaceous	Russia (Eastern)
Taxaceoxylon sp.	Afonin and Philippe (2014)	Early Cretaceous	Russia (Eastern)
Taxaceoxylon torreyanum (Shimakura) Kräusel & Jain	Shimakura (1936)	Pleistocene	Japan
Taxoxylon sp.	Dawson (1875)	Tertiary	Canada (Central)
Taxoxylon sp.	Mazen-Papier (1965)	Neogene	France
Taxus sp.	Stieber (1955)	Miocene	Hungary
Taxus sp.	Castañeda-Posadas et al. (2009)	Miocene	Mexico

Table 7
The post-Paleozoic Indian record for fossil woods with helical thickenings. Information on location and ages has been up-dated here to allow for geographic name changes and improvements in stratigraphic ranges (Tripathi, 2008; Weishampel et al., 2004). The attribution of these fossils to Taxaceae is questionable.

Specific names	Published	Provenance	Age given in the protologue	Actual age
Spiroxylon intertrappeum	Prakash and Srivastava (1959)	Dhar District, Madhya Pradesh, India	Early Tertiary	Berriasian–Aptian
Taxaceoxylon cupressoides	Sharma (1971)	Dhokuti, Santhal Pargana, Jharkhand	Middle Jurassic	Berriasian–Aptian
Taxaceoxylon sahnii	Rajanikanth and Sukh-Dev (1989)	Kota Fm, Chandrapur, Eastern Maharashtra	Middle Jurassic	Hettangian–Pliensbachian
Taxaceoxylon sp.	Lakhanpal et al. (1976)	Kota Fm, Chandrapur, Eastern Maharashtra	Early Jurassic	Hettangian–Pliensbachian
Taxaceoxylon sp.	Kräusel and Jain (1964)	Rajmahal Hills, Jharkhand	Early Cretaceous	Berriasian–Aptian
Taxoxylon rajmahalense	Bhardwaj (1952b)	Kulkipahar, Amrapara, Pakur district, Santhal Parganas, Jharkhand	Intertrappean beds (Rajmahal stage) Jurassic	Berriasian–Aptian
Taxoxylon sp.	Mahabale (1967)	Kota Fm., Pranhita/Godavari, Andhra Pradesh	Early Jurassic	Hettangian–Pliensbachian

If the *Cephalotaxus* Early Jurassic divergence from the rest of the Taxaceae is confirmed, it implies that abietinean TRP evolved at least twice within the Taxaceae: once in this genus and a second time in its sister group, the other Taxaceae. The Early Cretaceous age of the
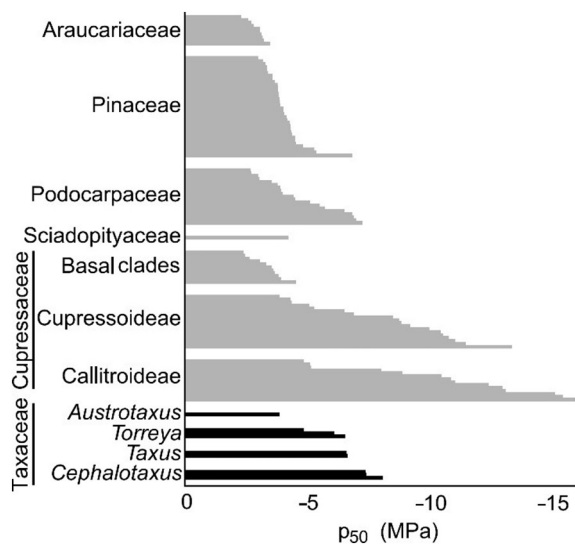
Fig. 6. Mean P_{50} values for the six conifer families. For the Taxaceae the mean values are provided by genera. Most extant conifers have a P_{50} ranging between −3 and −6 MPa. Values taken from Bouche et al. (2014), except for *Austrotaxus*, which comes from Larter (2016).
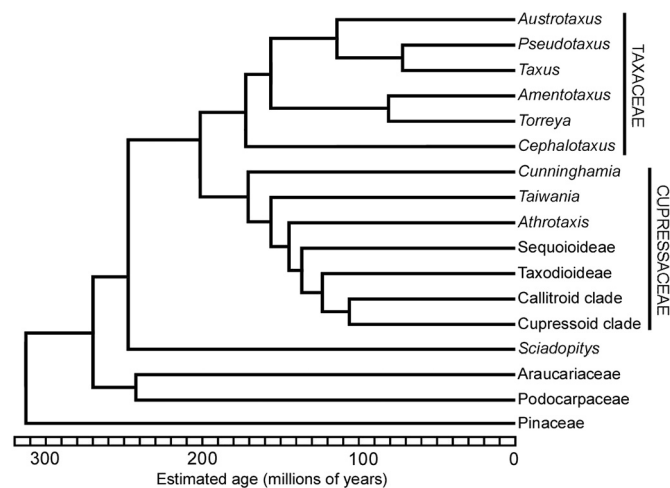
Fig. 7. Dated molecular phylogeny used to discuss Taxaceae fossil wood record, based on Leslie et al. (2018).

Cambodian *Protelicoxylon* (Table 5) is little substantiated, and might well be Middle to late Jurassic (Philippe et al., 2004). If so, the transition of the mixed type to the abietinean type of TRP in the *Cephalotaxus* sister-clade, as documented by the fossil record, would be more or less contemporaneous with the split of the two branches (*Torreya* + *Amentotaxus* and *Austrotaxus* + *Pseudotaxus* + *Taxus*). The Late Jurassic, during which this split might have taken place (Fig. 7), is well known as a time of global drying of Northern Hemisphere climates.

Taxaceae have probably been through several ecological bottlenecks during the Jurassic, which selected embolism-resistant taxa. This resistance was maintained when they acquired their typical wood, i.e. *Taxaceoxylon* features. This genus first appeared during the Early Cretaceous, a time when it was to be found in eastern continental Eurasia only, at relatively high paleolatitudes. This area is known to have been relatively dry at that time (Oh et al., 2011), with strongly influences of continental drought and the existence of an eastern coastal Cordillera. No Araucariaceae-like woods (i.e. genus *Agathoxylon*) are reported from this area at that time, while this type of wood was otherwise so common worldwide, possibly because of continental drought. Later, during the Late Cretaceous, at a time when North-America and Western Europe climates became more continental (Wolfe and Upchurch Jr, 1987), *Taxaceoxylon* spread to these two areas. It persisted there through the Cenozoic, and until now, with modern Taxaceae spanning most of the temperate boreal area, except for the high-latitudes that were probably their Cretaceous cradle.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2019.01.003.

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